

Cladonia luteoalba — an enigmatic Cladonia

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STENROOS, S. 1990: *Cladonia luteoalba* — an enigmatic Cladonia. — *Karstenia* 30:27–32.

The taxonomic status and podetial morphology of *Cladonia luteoalba* A. Wilson & Wheldon have been re-examined. The species commonly grows on podetia of other related lichens, in particular *C. coccifera* (L.) Willd., *C. borealis* Stenroos and *C. metacorrallifera* Asah., with which it is apparently able to form commensalistic symbioses. Its true podetia are escyphose, decorticate, rudimentary structures, never found with hymenia. Earlier, the podetia of the host lichens have been misinterpreted as podetia of *C. luteoalba*. The species comprises four major chemotypes: (1) the zeorin strain, (2) the barbatic acid strain, (3) the squamatic acid strain, and (4) the fumarprotocetraric acid strain. The distribution of the major chemotypes is mapped. The species is reported as new to Japan, China, India, Idaho and S. Finland.

Key words: Aromatic lichen substances, *Cladonia luteoalba*, lichen, taxonomy

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Introduction

Cladonia luteoalba A. Wilson & Wheldon (lichen-forming Ascomycotina) is known to be more variable chemically than most other members of the section *Cocciferae* (Delise) Evans. Its taxonomic status has been re-examined, because in recent revisions of the chemically variable *C. coccifera* (L.) Willd., s.lat. and *C. miniata* G. Meyer, s.lat., (Stenroos 1989a, b, c), these taxa could be divided into several chemically and morphologically readily distinguishable species.

C. luteoalba was described from West Lancashire and Westmorland, England (Wilson & Wheldon 1909), but it became more widely known only several decades later (e.g. Ahti 1965, 1985, Dahl & Krog 1970, Krog 1971, Kristinsson 1972, Østhagen 1974, Alstrup 1979, Tønnsberg 1979, Hansen 1982, Hansen & Fosaa 1985). Its status was doubted by Sandstede (1931, 1938), who placed it under *C. digitata* (L.) Schaerer, but other authors have regarded it as a distinct species.

Material and methods

Altogether c. 200 specimens of *Cladonia luteoalba* from the following herbaria were studied morphologically: BG, BM, H, O, TNS, TRH, TUR, UPS. Sixty-four of them were also analysed chemically by thin-layer chromatography (TLC), by the standard methods of C.F. Culberson (1972; solvent A) and White and James (1985; solvent B); see also Østhagen (1972). Additional chemical data were obtained from the annotations on the specimens (based on analyses by H. Østhagen, T. Tønnsberg and A. J. Sørensen Schei, in particular).

Chemistry

Ahti (1965) was the first to analyse *Cladonia luteoalba* chemically. He reported usnic acid and an unidentified substance (referring possibly to either zeorin or porphyrilic acid, which are both present in his specimen). Later, as many as nine secondary sub-

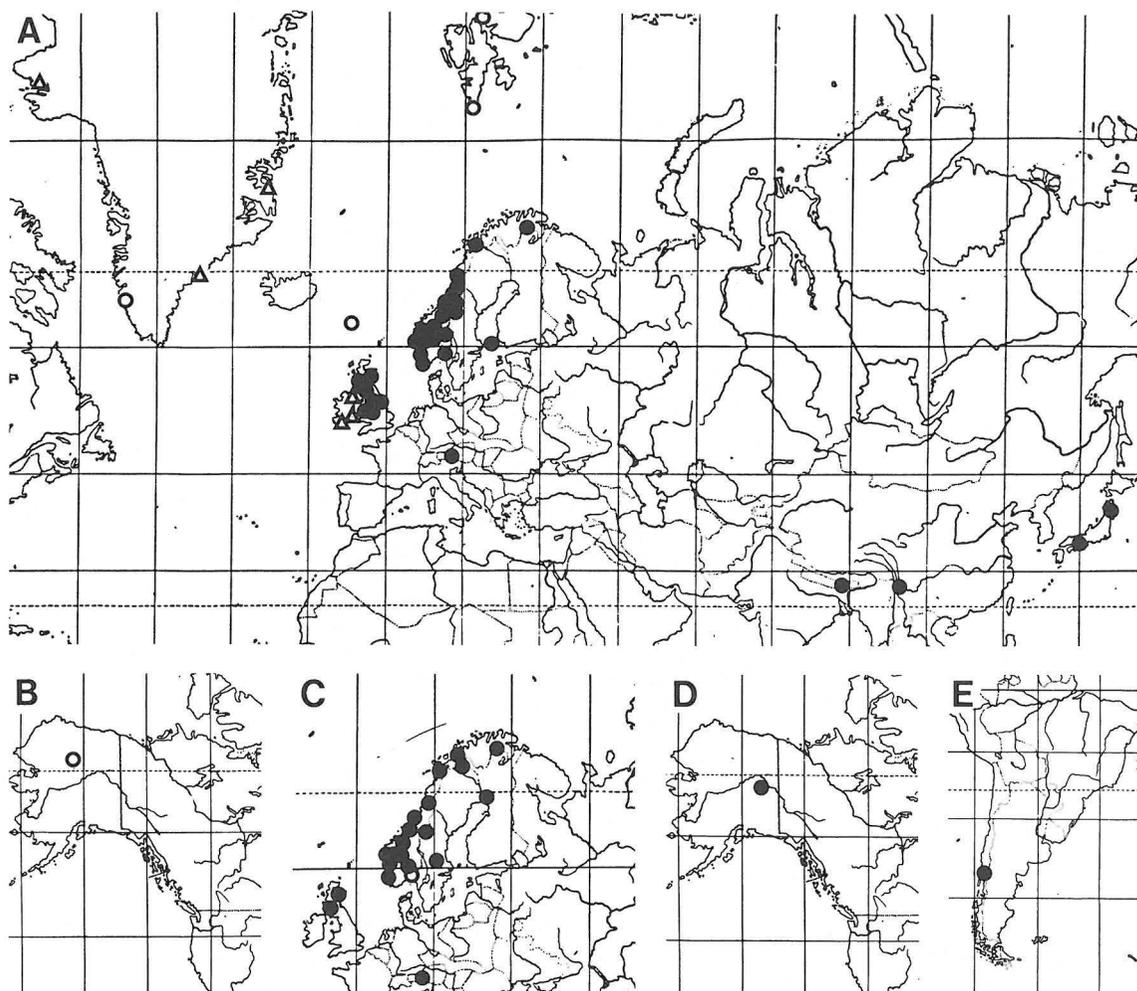


Fig. 1. The distribution of different chemotypes of *Cladonia luteoalba*. — A, B: zeorin strain. — C–E: squamatic acid strain. The localities marked with open circles are based on Dahl & Krog (1970), Østhaugen (1972), Alstrup (1979), and Tønnsberg (1979). The localities marked with open triangles belong to specimens for which no chemical data were given (Hansen 1982, 1986, 1989, Seaward 1984).

stances have been identified in *C. luteoalba*. On the basis of the major compounds, four major chemotypes can be distinguished, whose chemical variation shows a replacement pattern (see W.L. Culbertson 1970). These are (1) the zeorin strain, with accessory porphyritic acid and "conporphyritic" acid (see Nourish 1977; "unknown with porphyritic" in Østhaugen 1972), (2) the squamatic acid strain, with accessory didymic acid, (3) the barbatic acid strain, with accessory 4-O-demethylbarbatic acid and (4) the fumarprotocetraric acid strain (Østhaugen 1972, Nourish 1977, Krog et al. 1980 and Huovinen et al. 1989). Usnic acid

is constantly present in all chemotypes and is found in great abundance (11% of lichen dry weight in a specimen studied by Huovinen et al. 1989). In the zeorin strain four additional unidentified minor components were recognized in a HPLC analysis (Huovinen et al. 1989: fig. 2).

In the present study the following additional accessory substances were found: consquamatic acid (together with squamatic acid in chemotype 2; see Archer 1986), protocetraric acid and the substances Cph-1 and Cph-2 (together with fumarprotocetraric acid in chemotype 4) and isousnic acid (in chemotype

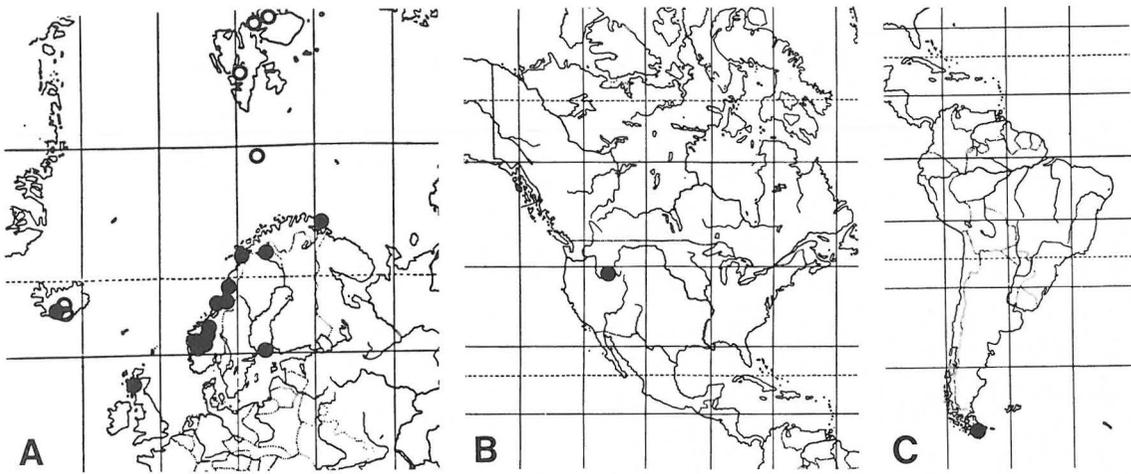


Fig. 2. The distribution of different chemotypes of *Cladonia luteoalba*. — A, B: barbatic acid strain. — C: fumarprotocetraric acid strain. The localities marked with open circles are based on Kristinsson (1972) and Østhagen (1972).

1), which was found in three specimens (China, Ahti *et al.* 46450 in H; Japan, Kurokawa 540492, 59291 in TNS).

The zeorin containing chemotype clearly exceeds the others in frequency. Of all the specimens studied, 61% belong to this strain (59% of these contain porphyrilic acid), while 25% belong to the squamatic acid strain (55% of these contain didymic acid), 13% to the barbatic acid strain and only 1% to the fumarprotocetraric acid strain. The different distributional tendencies of the chemotypes are shown in Figs. 1–2.

Rhodocladonic acid, which is characteristic of most members of the section *Cocciferae*, was not detected in this study, though it has been reported by Østhagen (1972) and Nourish (1977). Moreover, a yellow pigment, stated to be accessory in *C. luteoalba* by Østhagen (1972), was not recorded.

Morphology

Cladonia luteoalba is readily recognized by its conspicuous yellow thallus. Being generally sterile, however, i.e. producing only primary squamules (often few in number), it may easily be overlooked.

The primary squamules are large, recurved (when dry) to expose the bright yellow lower surface (see detailed descriptions in Østhagen 1972 and Krog *et al.* 1980, both including photographs; photographs have also been published by Hansen & Fosaa 1985 and Hansen 1986).

On the lower surface of the squamules is a thick, loose, cottony-arachnoid, yellow layer (below the

white medulla), consisting of short, entangled hyphae (c. 7–10 μm thick; Fig. 3). The surface of the hyphae appears to be encrusted with granules (crystals?), which is not the case in the medullary hyphae of *C. luteoalba*, or on the lower side of the squamules of, e.g., *C. borealis* Stenroos. This unusual tissue was called sorediate by Ahti (1965), but no truly soredium-like structures are present (no algae were found in the layer), although the hyphae or bunches of hyphae seem very easily to become detached from the surface.

Very few of the specimens include podetia. According to the descriptions (e.g., Østhagen 1972: fig. 1) the podetia bear wide scyphi, greatly resembling those of the *C. coccifera* group. A number of specimens with such podetia were in fact found in the present study. In several specimens, however, another type of podetium (although often rather poorly developed) can be observed. The latter type is escyphose (or with a very indistinct, narrow, scyphoid structure), and its podetial surface is ecorticate, with a thin, yellow, cottony layer of hyphae on the surface, similar to those in the primary squamules.

The two different podetial types do not correlate with the chemistry — both are present in all major chemotypes. All podetia which bear wide scyphi seem to be senile or even decayed (but, nevertheless, have large, young squamules growing on or inside the scyphi). Moreover, these podetia seem to grow from primary squamules that do not have the yellow lower surface characteristic of *C. luteoalba*, but greatly resemble the squamules of, for instance, *C.*

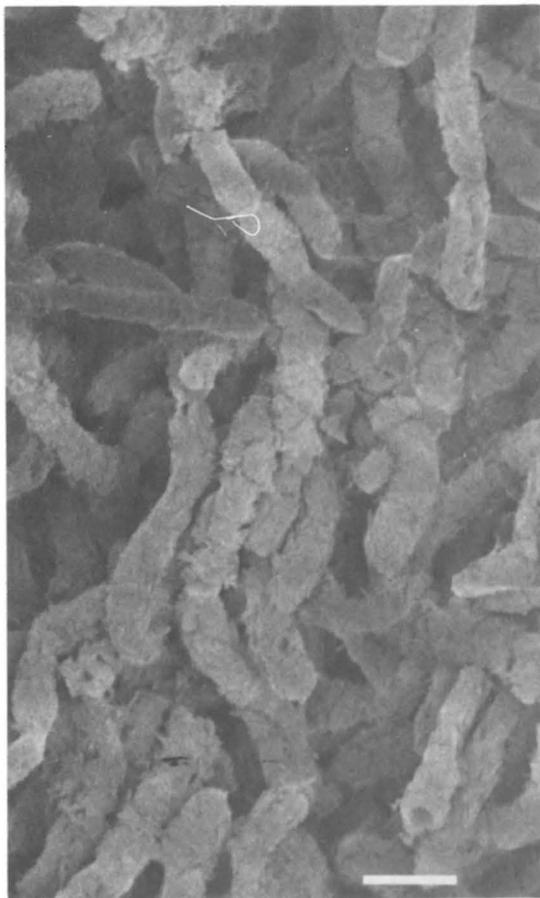


Fig. 3. Lower surface of the primary squamules with entangled hyphae (*Rosentreter 4526*, H).

borealis or *C. coccifera*. The other (escyphose) podetial type very clearly grows from primary squamules which have the yellow lower surface, and young developmental stages of podetia were also observed (their ontogeny following types I or IV of Jahns & Beltman 1973).

In the wide scyphose type, three different kinds of podetia could be found. These were identical to the podetia of *C. coccifera* (L.) Willd. (e.g., *Tønshagen 1984a*; TRH), *C. borealis* Stenroos (e.g., *Sørensen 3400g*; O) and *C. metacorallifera* Asah. (e.g., *Østhagen 3283*; O). It should be noted that in each of these specimens both the podetia and the yellow primary squamules (analysed separately) contain zeorin, barbatic acid or squamatic acid, respectively — thus also being chemically similar to the three species mentioned above.

These findings lead to the following conclusions: (1) The wide scyphose podetia (excluding the squamules) do not belong to *C. luteoalba* but more likely to other species, viz. *C. coccifera*, *C. borealis* or *C. metacorallifera*. (2) *C. luteoalba* may grow on other lichens (as already reported by Østhagen 1974 and Hansen 1982), evidently preferring the common species of the *C. coccifera* group (Fig. 4A). (3) Despite their variable chemistry, the morphology of the specimens of *C. luteoalba* suggests that they all belong to a single species, whose podetia are of the escyphose type (Fig. 4B, C). The specimen from China, however, differs from the others in its elongated, deeply divided squamules.

One possibility is that mechanical hybridization (see Hawksworth 1988a) is involved, at least in those cases in which the substrate lichen is alive. An interesting question is how the chemotype is determined, especially in the mechanical hybrids. As already mentioned, no examples could be found of specimens with mixed chemotypes. What is the "true" chemical composition of *C. luteoalba*, if squamules which grow on *C. metacorallifera* produce squamatic acid, those on *C. borealis* barbatic acid, etc.? It appears unlikely that the chemotypes of *C. luteoalba* are each specialized to hybridize mechanically with a species containing the same substances. However, it seems clear that *C. luteoalba* also grows "alone", i.e., on other substrates.

A more plausible explanation is commensalistic symbiosis, i.e. *C. luteoalba* belongs to the system of two mycobionts on one photobiont, in which a lichicolous mycobiont initially parasitizes an existing lichen (the loose hyphae on the lower side of the squamules possibly acting as vegetative propagules), taking over the photobiont to produce a mutualistic thallus of its own (see Hawksworth 1988b). This hypothesis also raises the question how much the photobiont affects the production of secondary substances in lichens (C.F. Culbertson & Johnson 1985).

One of the specimens with fumarprotocetraric acid, collected from Tierra del Fuego, probably grows on *C. lepidophora* Ahti & Kashiwadani, (which is known to have a strain containing fumarprotocetraric acid), but the material is too meagre for definite determination.

The possibility that *C. luteoalba* is not a distinct lichen at all, but a mere "disease", causing the basal squamules to enlarge and produce the yellow layer of loose cottony hyphae, can be ruled out because of the occasional production of conidiomata and characteristic true podetia, clearly belonging to the lichen.

It is commonly believed that *C. luteoalba* belongs to the section *Cocciferae*. No well-developed hyme-

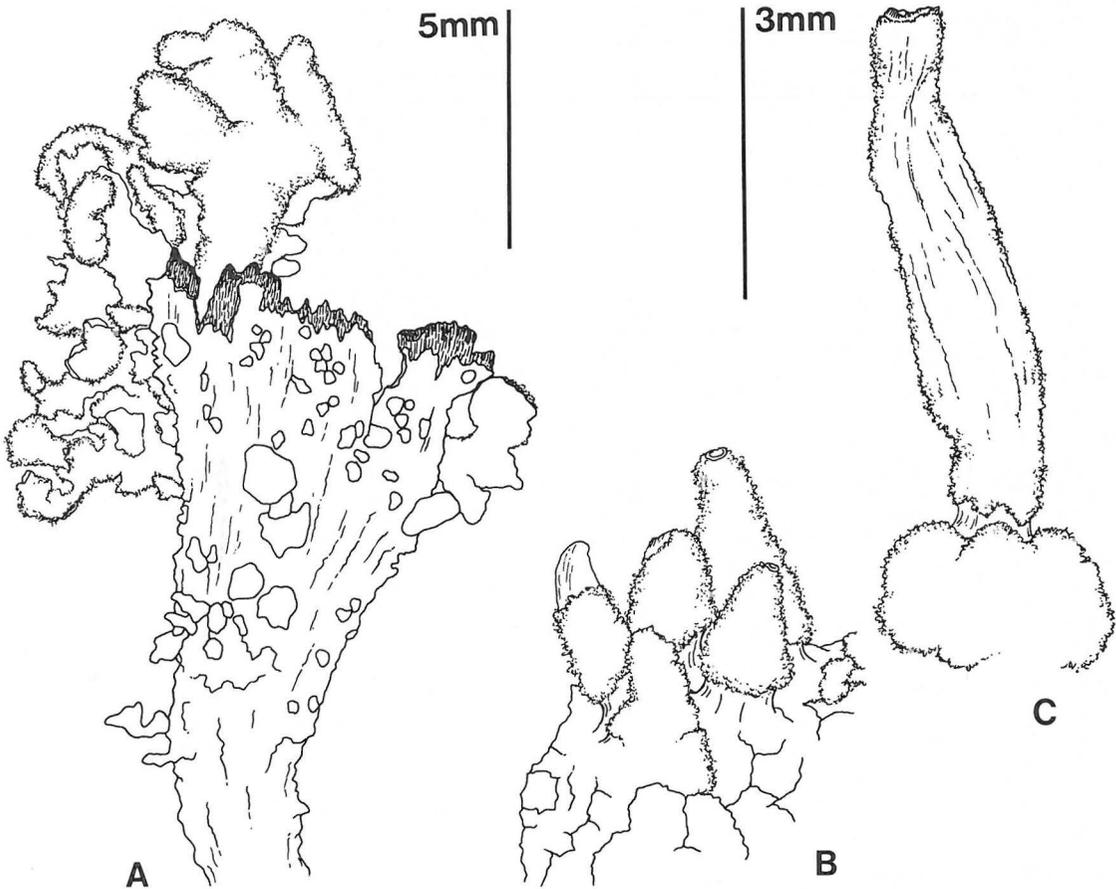


Fig. 4. General habit of *Cladonia luteoalba*. — A: primary squamules of *C. luteoalba* growing on a podetium of *C. borealis* Stenroos (Rosentreter 4526, H). — B, C: different developmental stages of podetia (B, Tønberg s.n., TRH; C, James s.n., BM).

nial discs could be found, but judging from some podetial tips, it is possible that *C. luteoalba* is pale-fruited, thus belonging to the subsection *Ochroleucae* (Fr.) Mattick of the section *Cocciferae*. Chemically, it is clearly a member of *Cocciferae*.

Distribution

According to the present collections, *Cladonia luteoalba* is most common in Northwest Europe. It is somewhat oceanic, and its range can be expected to be more or less circumpolar in the Northern Hemisphere (see also Østthagen 1974). Most collections seem to come from the northern boreal (upper oroboreal) to arctic (oroarctic) zone, but it has been found down to the hemiboreal and northern temperate zones. *C.*

luteoalba belongs to the bipolar element, which is well represented among the Cladoniaceae in Tierra del Fuego (Stenroos 1987). Maps have been published by Dahl and Krog (1970) and Østthagen (1971, 1972).

C. luteoalba is reported here as new to the USA (excluding Alaska), India, China, Japan and southern and central Finland. The four major chemotypes have clear differences in their distribution, the zeorin strain being the most widespread one (Fig. 1A, B). The presence or absence of didymic acid (in the squamatic acid strain) and porphyritic acid (in the zeorin strain) are not expected to have any great significance in this context, but the material from many regions is too scarce for definite conclusions. Moreover, the presence or absence of an accessory substance may also be due to varying conditions during

analysis or different determinations of the substance, especially when it occurs in low amounts.

In addition to lichens, *C. luteoalba* grows on mosses, plant debris, peat, thin soil (preferring acid conditions) and soil in snowbed communities. It is often found in sunny sites, although it also thrives in shady localities (Østhagen 1971, 1972, Øvstedal 1972, Alstrup 1979 and Krog et al. 1980).

Selected specimens examined

Finland. *Ahvenanmaa:* Jomala, Mellangadd, 1952 *Mäkinen* (TUR). Brändö, Korsö, 1988 *Puolasmaa* (TUR). *Perä-Pohjanmaa:* Ylitornio, Takainen Rovavaara, 1988 *Halonen & Hyvärinen* (OULU).

India. *Sikkim:* 1 830 m, *Hooker 2102* (BM).

China. *Yunnan:* Lijiang Co., Yulongshan, 3 050 m, 1987 *Ahti et al. 46450* (H).

Japan. *Honshu:* Rikuchu Prov., Mt. Hayachine, 1 300–1 900 m, 1959 *Kurokawa 59291* (TNS). Settsu Prov., Mt. Rokko, 1954 *Kurokawa 540492* (TNS).

U.S.A. *Idaho:* Custer Co., Middle Fork of Salmon River, 1987 *Rosentreter 4526* (H).

Acknowledgements. My sincere thanks are due to Prof. Teuvo Ahti for critical reading of the manuscript. The help of the keepers of the herbaria from which I borrowed specimens is also gratefully acknowledged. I am especially indebted to Mr. Arto Puolasmaa (Turku) for sending me valuable material on loan and to Ms. Vanamo Salo for her help in SEM. Ms. Anna A. Damström, M.A., revised the English language.

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Received on 20 January 1990